

Crane Biology



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Cranes, an ancient family of birds, have graced our planet's skies and stalked the grasslands and wetlands for at least 40 million years. The fossil record includes at least 17 extinct species, many of which were closely related to African Crowned Cranes (Brodkorb 1967). No crane species has become extinct within recorded history. Fifteen species (Figs. 1.1–1.16) and 14 recognized subspecies survive (Table 1.1).

There have been four comprehensive volumes written about the biology of the world's 15 species of cranes (Blaauw 1897; Makatsch 1970; Walkinshaw 1973; Johnsgard 1983). In addition, there have been comprehensive single species accounts on Sandhill Cranes (Walkinshaw 1949), Whooping Cranes (Allen 1952; McNulty 1966; Doughty 1989), Red-crowned Cranes (Masatomi 1970–1974), and Siberian Cranes (Sauey 1985). Major contributions on Black-necked Cranes (Bishop 1994), Grey Crowned Cranes (Gichuki 1995), and Blue Cranes (Allan 1995) will soon be available.

Special centers for crane research provide an abundance of published and unpublished information about the husbandry of cranes. These include the Department of the Interior's Patuxent Wildlife Research Center (11510 American Holly Drive, Laurel, MD 20708-4019), International Crane Foundation (E-11376 Shady Lane Road, Baraboo, WI 53913-0447), Oka State Nature Reserve (391072 Lakash, Spasskogo Raiona, Ryazanskoi Oblasti, Okskii Zapovednik, Russia), Vogelpark Walsrode (D-3030, Walsrode, AM Rieselbach, Germany), Kushiro Crane Park (c/o Kushiro Zoo, 11 Ninishibetu Akan Cho, Akan Gun, Hokkaido, Japan), Serendip Research Center (P.O. Box 2, Lara, Victoria, 3212, Australia), Beijing Zoo (137 Xi Zhi Men Wai St., Beijing, China 100044), Shenyang Center for the Study, Preservation, and Breeding of Cranes (No. 1, Wanquan St., Dadong District, Shenyang, China 110015), and the Conservation and Research Center of the Smithsonian Institution (The Wildlife Survival Center, Front Royal, VA 22630).

The Ron Sauey Memorial Library for Bird Conservation at the International Crane Foundation (ICF) is a repository for the world's literature on cranes and their habitats. Ron Sauey was a co-founder of the International Crane Foundation. In 1987, at the age of 37, he tragically passed away as a consequence of a cerebral hemorrhage. The construction of the library was supported by the Sauey family in memory of Ronald. The library contains English translations of the most important non-English publications. The library is connected by modem to the library system of the University of Wisconsin and can be accessed at the following telephone number: 1-608-262-8670.

Natural History

Taxonomy

Cranes are found on five continents. There is no evidence that cranes ever inhabited South America. The current concentration of crane species in Asia and Africa suggests an Old World origin of Gruinae, with a more recent colonization of Australia and North America (Archibald 1976a). Most fossil species, however, have been found in North America (Brodkorb 1967), reflecting both the proportionately greater amount of paleornithological work in North America (Archibald 1976a) and the possible origins of cranes in the West. Krajewski (1988), however, believes that cranes originated in Europe near the end of the Paleocene Epoch.

All cranes are in one of two subfamilies, Balearicinae or Gruinae, in the family Gruidae. The two species of African Crowned Cranes are placed in the subfamily *Balearicinae* (Peters 1934). They are distinguished from other species by their ability to roost in trees, and their loose plumage, straight trachea, elaborate crests, and colorful facial markings. The inability to tolerate extended periods of freezing temperatures perhaps led to the extinction

TABLE 1.1

World species and subspecies of cranes and their geographic distribution (Walkinshaw 1973).

COMMON NAME	SCIENTIFIC NAME	DISTRIBUTION
Family Gruidae		
Subfamily Balearicinae		
Black Crowned Crane	<i>Balearica pavonina</i>	
West African Crowned Crane	<i>B. p. pavonina</i>	West Africa
Sudan Crowned Crane	<i>B. p. ceciliae</i>	Central Africa
Gray Crowned Crane	<i>Balearica regulorum</i>	
East African Crowned Crane	<i>B. r. gibbericeps</i>	East Africa
S. African Crowned Crane	<i>B. r. regulorum</i>	Southern Africa
Subfamily Gruinae		
Wattled Crane	<i>Bugeranus carunculatus</i>	Africa
Blue Crane	<i>Anthropoides paradisea</i>	Southern Africa
Demoiselle Crane	<i>Anthropoides virgo</i>	Asia, Africa
Siberian Crane	<i>Grus leucogeranus</i>	Asia
Sandhill Crane	<i>Grus canadensis</i>	
Lesser Sandhill Crane	<i>G. c. canadensis</i>	East Siberia Arctic N. America
Canadian Sandhill Crane	<i>G. c. rowani</i>	Boreal Canada
Greater Sandhill Crane	<i>G. c. tabida</i>	Northern USA
Florida Sandhill Crane	<i>G. c. pratensis</i>	Southeast USA
Mississippi Sandhill Crane	<i>G. c. pulla</i>	Mississippi
Cuban Sandhill Crane	<i>G. c. nesiotis</i>	Cuba
White-naped Crane	<i>Grus vipio</i>	East Asia
Sarus Crane	<i>Grus antigone</i>	
Indian Sarus Crane	<i>G. a. antigone</i>	India
Eastern Sarus Crane	<i>G. a. sharpii</i>	Southeast Asia
Australian Sarus Crane	<i>G. a. gilli</i>	Australia
Brolga	<i>Grus rubicunda</i>	Australia
Eurasian Crane	<i>Grus grus</i>	
European Crane	<i>G.g. grus</i>	Europe, west Asia
Lilford's Crane	<i>G. g. lilfordi</i>	East Asia
Hooded Crane	<i>Grus monacha</i>	East Asia
Black-necked Crane	<i>Grus nigricollis</i>	Tibetan Plateau
Red-crowned Crane	<i>Grus japonensis</i>	East Asia
Whooping Crane	<i>Grus americana</i>	North America

of Crowned Cranes on the northern continents during the Pliocene Epoch. Today, the two surviving species inhabit the wetlands and savannas of Africa. Paleontological, anatomical, behavioral, and DNA studies all indicate that Crowned Cranes are closest to the ancestral stock that gave rise to the more recent subfamily *Gruinae* (Archibald 1976a; Wood 1979; Krajewski 1988) which includes the other 13 species.

The 13 species of *Gruinae* were traditionally divided into three genera: *Bugeranus*, *Anthropoides*, and *Grus*. Recent DNA hybridization studies, however, suggest that *Anthropoides* and *Bugeranus* should be merged with *Grus* (Ingold 1984; Krajewski 1988). *Grus* includes four distinct groups of closely related species: the Sarus Species Group (White-naped, Sarus, Brolga), the Whooping Crane Species Group (Eurasian, Hooded, Black-necked, Red-crowned, Whooping Crane), and the Sandhill Crane and the Siberian Crane which each stand alone. The Sandhill Crane is probably most closely allied to the Sarus Group (Archibald 1976a). Ethology and anatomy weakly link the Siberian Crane to the Wattled Crane (Archibald 1976b; Wood 1979), but DNA and recent behavior work suggest that the Wattled Crane and *Anthropoides* (Demoiselle and Blue) are closely related (Krajewski 1988; Ellis et al. *in prep*), and that the Siberian Crane is distinct from many of the other *Gruinae* species groups and should perhaps be placed in a separate genus (Krajewski 1988).

Food Habits

Cranes are omnivorous and some species rely heavily on aquatic foods (Walkinshaw 1973). Most cranes probe the subsurface with their bills and take foods

from the soil surface or vegetation. Young chicks are fed by their parents and gradually become more independent in their feeding until they separate from the parents prior to the next breeding season. During these first 10 months of development, captive cranes are extremely inquisitive. Perhaps this drive to investigate novel objects helps them discover food items in the wild.

Sandhill Cranes feed primarily on small grains (corn, wheat, barley, and sorghum) in fall, winter, and spring, but during the nesting season (when they associate more with wetlands), the greater part of the diet consists of crayfish, plant tubers, chufa, rodents, frogs, berries, bird's eggs, and nestlings (Walkinshaw 1949; Lewis 1974; Bennett 1978; Mullins and Bizeau 1978; Iverson et al. 1982; Herter 1982). Summer foods of the Whooping Crane include frogs, minnows, berries, and large nymphal and larval forms of insects (Allen 1956; Novakowski 1966). Principal winter foods of Whooping Cranes include blue crabs, clams, marine worms, amphibians, crayfish, fish, snails, insects, and sedge tubers found in coastal marshes and estuaries, but these cranes also feed in uplands on berries, acorns, insects, and small vertebrates (Allen 1952; Uhler and Locke 1969; Hunt and Slack 1987).

The 15 crane species can be divided into several groups based on the habitats in which they feed during the breeding and nonbreeding season (Table 1.2). The less common species worldwide, like the Whooping Crane, Siberian Crane, Wattled Crane, Red-crowned Crane, Black-necked Crane, and White-naped Crane, are more dependent on aquatic habitats throughout the year and not just during the breeding season.

TABLE 1.2

Breeding and nonbreeding season food habits of cranes.

HABITAT	BREEDING SEASON	NONBREEDING SEASON
Primarily feeding in uplands	Demoiselle, Blue Cranes	Crowned, Demoiselle, Blue, Sandhill, Eurasian Cranes
Feeding in both uplands and wetlands	Crowned, Sandhill, Sarus, Eurasian, White-naped, Black-necked Cranes, Brolga	Sarus, White-naped, Red-crowned, Black-necked, Hooded Cranes, Brolga
Primarily feeding in wetlands	Wattled, Siberian, Hooded, Red-crowned, Whooping Cranes	Wattled, Siberian, Whooping Cranes

A Color Signature of Cranes Around the World

FIGURE 1. *Black Crowned Crane.*
PHOTO BY DAMIAN DEBSKI

FIGURE 2. *Gray Crowned Crane, Zambia.*
PHOTO BY L. H. WALKINSHAW

FIGURE 3. *Wattled Cranes, Wakkerstroom, South Africa.*
PHOTO BY WARWICK TARBOTON

FIGURE 4. *Blue Cranes, Wakkerstroom, South Africa.*
PHOTO BY WARWICK TARBOTON

FIGURE 5. *Demoiselle Cranes.*
PHOTO BY J. H. DICK

FIGURE 6. *Siberian Crane at Keoladeo National Park, India.*
PHOTO BY ICF

FIGURE 7. *Sandhill Crane, Wisconsin.*
PHOTO BY GEORGE W. ARCHIBALD

FIGURE 8. *White-naped Crane at Zhalong, China.*
PHOTO BY STURE KARLSSON

FIGURE 9. *Sarus Cranes Unison-call at Bharatpur, India.*
PHOTO BY M. PHILLIP KAHL

FIGURE 10. *Brolgas, Queensland, Australia.*
PHOTO BY GEORGE W. ARCHIBALD

FIGURE 11. *Eurasian Cranes at Zao Hai, China.*
PHOTO BY GEORGE W. ARCHIBALD

FIGURE 12. *Hooded Cranes at Izumi, Japan.*
PHOTO BY STURE KARLSSON

FIGURE 13. *Black-necked Cranes at Cao (or Zao) Hai, China.*
PHOTO BY GEORGE W. ARCHIBALD

FIGURE 14. *Red-crowned Cranes.*
PHOTO BY TERA0 SATO

FIGURE 15. *Whooping Cranes at Aransas National Wildlife Refuge, Texas.*
PHOTO BY MARY BISHOP

FIGURE 16. *Demoiselle Cranes captured on migration in Pakistan are eaten or rendered flightless and tamed.*
PHOTO BY STEVEN E. LANDFRIED



FIG. 1.1. *Black Crowned Crane* (*Balearica pavonina*).

PHOTO DAMIAN DEBSKI



FIG. 1.2. *Gray Crowned Crane* (*Balearica regulorum*), *Zambia*.

PHOTO L. H. WALKINSHAW



FIG. 1.3. *Wattled Cranes (Bugeranus carunculatus), Wikkertstroom, South Africa.*

PHOTO WARWICK TARBOTON



FIG. 1.4. *Blue Cranes (Anthropoides paradisea), Wakkerstroom, South Africa.*

PHOTO WARWICK TARBOTON



FIG. 1.5. *Demoiselle Cranes (Anthropoides virgo)*.

PHOTO J. H. DICK



FIG. 1.6. *Siberian Crane* (*Grus leucogeranus*) at *Keoladeo National Park, India, 1982.*

PHOTO ICF



FIG. 1.7. *Sandhill Crane* (*Grus canadensis*), *Wisconsin*.

PHOTO GEORGE W. ARCHIBALD



PHOTO STURE KARLSSON

FIG. 1.8. *White-naped Crane (Grus vipio) at Zhulong, China.*



FIG. 1-9. *Sarus Cranes (Grus antigone) Unison-call at Bharatpur, India, 1967.*

PHOTO M. PHILLIP KAHL



FIG. 1.10. *Brolgas* (*Grus rubicunda*), Queensland, Australia.

PHOTO GEORGE W. ARCHIBALD



FIG. I.II. *Eurasian Cranes (Grus grus) at Zao Hai, China.*

PHOTO GEORGE W. ARCHIBALD



FIG. 1.12. Hooded Cranes (*Grus monacha*) at Izumi, Japan.

PHOTO STURE KARLSSON



FIG. 1.13. *Black-necked Cranes (Grus nigricollis) at Cao (or Zao) Hai, China.*

PHOTO GEORGE W. ARCHIBALD



FIG. 1.14. *Red-crowned Cranes (Grus japonensis)*.

PHOTO TERAO SATO



FIG. 1.15. Whooping Cranes (*Grus americana*) at Aransas National Wildlife Refuge, Texas.

PHOTO MARY BISHOP



FIG. 1.16. *This Demoiselle crane, captured on migration in Pakistan, became a pet.*

PHOTO STEVEN E. LANDFRIED

Plumage Coloration

Crane chicks (Fig. 1.17) are first covered with natal down which is largely concealed or replaced by juvenal plumage by fledging time (Stephenson 1971). During the first few weeks, the legs and neck of a crane chick grow proportionately faster than the wings. Juvenile cranes are either predominantly reddish brown (Crowned, Siberian, White-naped, Sandhill, Red-crowned, and Whooping Cranes) or gray (Demoiselle, Blue, Wattled, Sarus, Eurasian, Hooded, and Black-necked Cranes, and Brolgas). The juvenile colors probably provide anti-predator camouflage.

Adult cranes are either white, gray, black, or combinations thereof. White cranes inhabit vast open wetlands where excellent visibility makes white birds extremely apparent. Being white may help territorial pairs become more obvious to potential intruders and thus minimize the amount of time and energy spent in aggressive encounters. The gray cranes occupy smaller wetlands that are often partially or completely covered by trees. Terrestrial predators are undoubtedly more of a threat in forested wetlands than on open wetlands. The gray color helps the crane conceal itself in the marsh and on the nest.



FIG. 1.17. An 11-day-old Sandhill Crane.

PHOTO GLEN SMART

Sandhill and Eurasian Cranes also perform feather painting that may provide further protective coloration especially for incubating adults. In early spring, they paint their feathers with mud, the iron oxides of which penetrate and permanently stain the feathers a rust color (Taverner 1929).

Social Behavior

Cranes have a wide variety of vocal and visual displays (Ellis et al. *In prep.*). The African Crowned Cranes have rather simple loud “honking” calls. The Siberian Crane has a high-pitched, flute-like call, whereas Wattled Crane calls are high-pitched but raspy. Demoiselle, Blue, and Sandhill Cranes have low, broken calls, and the remaining species have shriller calls. The trachea of Gruinae cranes coils within, and fuses with, the sternum to varying degrees in each species (Blaauw 1897). Tracheal development is greatest in the Whooping Crane Species Group, and the pitch of the calls in these species is higher than in most other cranes. The trachea and sternum amplify the calls produced in the larynx (Prange et al. 1985).

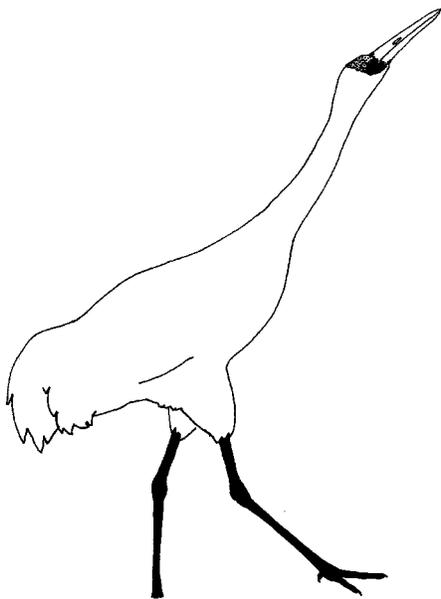
Crane calls include low, purr-like Contact Calls, slightly louder Pre-flight Calls, purr-like or shrill Pre-copulatory Calls, groan-like or scream-like Distress Calls, scream-like plaintive Location Calls, abrupt Alarm Calls, and loud Flight Calls and Guard Calls. Crane calls also include loud, complex duets called Unison Calls (Allen 1952; Masatomi and Kitagawa 1975; Archibald 1976a, 1976b; Voss 1976) which have both sexual and threat functions (Archibald 1976a).

Plumage-wise, cranes are sexually monomorphic, but the vocal and visual components of the Unison Call (an antiphonal duet) are sexually distinct (Fig. 11C.1), the exceptions being the Black Crowned, Gray Crowned, and Siberian Cranes. Wattled Cranes seldom Unison Call, but when they do the male slightly elevates his wings above his back for a second at the end of the duet. In other cranes, the male typically emits a long series of low calls, and the female accompanies him with two or three high-pitched calls for each low call of the male. In Blue Cranes and the Sarus Species Group, the males invariably elevate their wings and droop their primaries during the Unison Call, while the females keep their wings closed. Demoiselle Cranes call with wings closed, but the female usually holds her neck back, slightly beyond

the vertical. Sandhill Cranes also call with closed wings, but in contrast to Demoiselle Cranes, the male holds his head close to the vertical position while the female calls with her beak horizontal. In Siberian Cranes and the Whooping Crane Species Group, the wings may be elevated in either sex depending on the intensity of the situation, with wing elevation being proportional to the level of threat or intensity of display.

Other social displays include rigid threat posturing, rigid Strutting, Ritualized Preening of the back or thigh, feather ruffling, Stamping, Flapping, tail fluttering, Crouching, Growling, and Hissing. Cranes also perform an elaborate dance involving Bowing, Leaping, Running and Flapping, tossing an object (often a feather) into the air, and more (see Chapter 6).

The form of the complex visual and vocal displays of cranes is apparently independent of learning or the species of the foster parent; these displays appear to be genetically determined. Even blind cranes in captivity are able to perform a full complement of crane behavior. The object at which the display is oriented, however, is learned. If a crane chick is reared by people, it will prefer to associate with people and not cranes. Learned species recognition is important in maintaining reproductive barriers between sympatric species. For example, White-naped Cranes and Red-crowned Cranes are sympatric on many of their nesting and wintering areas, but hybrids have not been reported in the wild.



Breeding Biology

Annual Cycle

The annual cycle of cranes can be divided into a 3–5 month nesting period and a longer non-breeding period. Many species (Demoiselle, Siberian, White-naped, Eurasian, Hooded, Black-necked, Red-crowned, Whooping, and three migratory subspecies of Sandhill Cranes) migrate hundreds, or even thousands, of kilometers between breeding and wintering grounds. Except for Wattled Cranes, which sometimes remain on nesting territories throughout the year (Tarboton 1984), all cranes become more gregarious during the non-breeding period and move to regions where food is abundant. Eurasian Cranes, and possibly Red-crowned Cranes, do not breed consistently every year, an aspect of crane biology that requires further research.

Pair Formation and Duration

Successful breeding depends on securing a compatible mate and a breeding territory. In the Sandhill Crane, unpaired males sometimes establish a breeding territory and wait for the arrival of a female. Unmated females, by contrast, search for a male that has an established territory (Nesbitt 1989).

In most cranes, breeding usually begins between ages 3 and 6. Whooping Cranes sometimes breed as early as age 3 (Kuyt and Goossen 1987), but most produce fertile eggs at age 4 or 5. Breeding, on average, occurs later in Whooping Cranes in captivity (Ellis et al. 1992). Sandhill Cranes begin breeding at ages 2 to 5 depending on subspecies and location (Radke and Radke 1986; Nesbitt and Wenner 1987; Tacha 1988; Nesbitt 1992). A young crane is perhaps more likely to breed when paired with an experienced breeder that has lost its mate.

In Sandhill Cranes, sub-adult pairings are usually ephemeral (Nesbitt 1989). Nesbitt and Wenner (1987) found that the average, sub-adult Sandhill Crane paired five times before successfully breeding, with pair bond duration related to the production of young. Pairing can be rapid, or it may require many months of interaction (Nesbitt and Wenner 1987). Unison Calling and dancing are particularly important in the development of pair bonds.

Although young pairs often sever ties at the end of a breeding season (Drewien 1973; Nesbitt and Wenner 1987), established pairs return to the same breeding territory each year and defend it vigorously. Unison Calls and chases are particularly frequent during the several weeks before eggs are laid. Territory size is extremely variable, ranging from a few to several hundred hectares, with territory size roughly proportional to the openness of the landscape (Johnsgard 1983).

Breeding Season

The crane breeding season is either associated with distinct seasonality in the higher latitudes or with the wet/rainy season in lower latitudes. For species that breed in arctic to north temperate regions (Siberian, Lesser Sandhill, Hooded, and Whooping Cranes), spring is so short that renesting is seldom possible. Mid-latitude breeders, however, frequently renest if the first attempt fails. Cranes breeding in tropical and subtropical regions (Crowned, Blue, and Sarus Cranes, and Brolgas) usually breed on seasonal wetlands created during the rainy season (Archibald and Swengel 1987; Konrad 1987). Crowned Cranes can nest in any month depending on the rains (Walkinshaw 1964; Brown and Britton 1980; Pomeroy 1980), Blue Cranes usually nest at the beginning of South Africa's rainy season in November or December, and Sarus Cranes nest during southern Asia's July to October monsoons. Brolgas in northern Australia breed during the January to March rainy season, while those in the south begin nesting in spring (September to October) (Walkinshaw 1973). Most of the Wattled Cranes in southern Africa breed during winter, from May to October (Konrad 1981; Johnsgard 1983; Tarboton 1984) and at the end of the dry season, although they may breed at any time of year in Natal (Cyrus and Robson 1980; Tarboton 1984).

Nests, Eggs, and Chicks

Grassland nesters (Demoiselle and Blue Cranes, and sometimes Brolgas) usually lay their eggs on the bare ground with a nest composed of only a few twigs or pebbles (Van Ee 1966; Winter 1991); most other cranes build a **low platform nest** (Fig. 1.18) in shallow water. Water depth and the nest size are closely related: the deeper the water, the larger the nest. During flooding, cranes rapidly add material to the nest to keep the eggs above water. Wattled Crane pairs will not breed if their wetland territory lacks a small shallow pond for



FIG. 1.18 *Sandhill Crane nest in Florida.*

PHOTO GENE KNODER

nesting, but if a small area of open water is created, they sometimes nest immediately (Johnson and Barnes 1991).

Crane **clutch size** varies from two to three eggs for Crowned Cranes, two eggs for most other species, and usually one egg for Wattled Cranes. Eggs of Crowned Cranes are a light bluish white. Sarus, Brolgas, and some Red-crowned Cranes have plain white eggs with a few speckles of green or gray. Eggs for other cranes are heavily spotted with a light to dark brown background. Although there is remarkable variation between species, crane eggs from hot climates usually have less pigmentation than those in cold climates.

Both sexes assist in incubation, and the female usually incubates at night (Walkinshaw 1965). Incubation exchanges take place several times during the day and are sometimes accompanied by Unison Calling (Voss 1976). These vocalizations can facilitate humans finding birds or nests. The incubation period varies from 29 days in Demoiselle and Siberian Cranes to as many as 34 days in Wattled Cranes (see Table 4.1). Except for Wattled Cranes, which abandon the second egg (rarely laid) after the first chick has hatched, most cranes incubate until all live eggs have hatched. If the eggs are infertile or added, cranes will sometimes incubate 30–50 days beyond projected hatch dates (Walkinshaw 1965).

Some Crowned Crane clutches hatch synchronously (Walkinshaw 1964), but there is a one-to-two-day interval between the hatching of chicks in most other species. Sibling rivalry is important in determining chick survival. One chick is usually dominant over its sibling, and the dominant chick gets most of the food from the parents. Fighting between chicks is somehow linked to hunger. If food is scarce, the subordinate chick usually perishes. Sibling aggression has been observed in Greater Sandhill Cranes (Littlefield and

Ryder 1968; Drewien 1973), but is less pronounced in Black-necked (Li et al. 1991), Florida Sandhill (Layne 1982), and Demoiselle Cranes, although chicks of the latter species frequently compete for parental feedings (Winter 1991). Sibling aggression is so severe in Siberian Cranes that there are few reports of a pair rearing two chicks. Because of aggression even when food is available *ad libitum*, it is very difficult to captive-rear Whooping Crane chicks in groups. Two wild chicks are sometimes reared with each adult leading a chick on separate, but nearby, paths.

Species nesting in ephemeral wetlands (Crowned and Demoiselle Cranes) or in the Arctic where the nesting season is brief (Siberian, Lesser Sandhill Cranes) have shorter pre-fledging periods than species that inhabit permanent wetlands (Wattled Cranes) or regions with longer growing seasons. Immature cranes remain with their parents for 8–10 months until the onset of the next breeding season (Alonso et al. 1984). An abrupt change in the chick's voice from high frequency "peep-like" calls to the loud deeper voice of the adult coincides with the period during which the chick either leaves its parents of its own volition or is driven off (Nesbitt 1975; Nesbitt and Archibald 1981; Alonso et al. 1984).

After leaving their parents, young cranes gather in flocks with other non-breeders and move to foraging and roosting sites where they remain while the adults breed elsewhere (Kuyt 1979). Later they are joined by unsuccessful mated pairs and eventually by family groups. At approximately 18 months of age, a young crane exhibits **adult-like social behavior** including well-developed epigamic sign stimuli (e.g., red crown or fully grown wattles), threat displays, Guard and Unison Calls, and dancing (Bishop 1984; Nesbitt and Wenner 1987). Pairing can occur from this time onward.

Cranes in Captivity

Since ancient times, people have been fascinated by cranes and have kept them in captivity (Derrickson and Carpenter 1987). Cranes are depicted on the temple walls of the Egyptians (Whymper 1909), and cranes were raised by Chinese royalty more than 2,200 years ago (Cheng 1981). Continuing in the tradition of their ancestors, Africans today take wild chicks, raise them, and keep them as pets. In Australia, hand-raised Brolgas, popular pets, are sometimes called "Native

Companions." Thousands of Demoiselle and Eurasian Cranes are trapped during migration through the passes of the Hindu Kush mountains of Pakistan; many are eaten, others are sold as pets (Fig. 1.16). Cranes have always been popular in zoos in Europe and in the Orient (Johnsgard 1983:51).

Japan's "Mr. Zoo," Dr. Tadamichi Koga, was the first to treat the captive management of cranes in a scientific manner. Prior to the Second World War, Japanese zoos imported wild cranes from the mainland. During the war most of the zoo animals perished, and after the war importation was no longer possible. Unless cranes could be induced to breed in captivity, there would soon be no cranes for Japanese zoos. Dr. Koga noticed that if cranes lose their eggs, they rapidly re-egg, and by collecting and then artificially incubating the eggs, several clutches could be produced from a single pair (Koga 1961, 1976). Resulting chicks were hand-raised and then distributed to zoos throughout Japan.

About the same time, Dayton Hyde (1957) noted that cranes usually lay two eggs but rarely raise two young. He suggested that a **captive Whooping Crane flock could be established** without detriment to the wild population **by removing one egg** from each clutch. Using this reasoning, about 400 Whooping Crane eggs have been removed from the Wood Buffalo population in Canada from 1967 to the present. Productivity data, before and during this era, suggest that this egg harvest may have actually increased the number of chicks fledged each fall in Canada (Kuyt 1987; F. G. Cooch, Migratory Birds Branch, Ottawa, Ontario, Canada, personal communication).

Following Dr. Koga's example, several **crane propagation centers** have been established in recent decades. In 1966, the U.S. Fish and Wildlife Service, in cooperation with the Canadian Wildlife Service, established a captive breeding center for Whooping Cranes at Patuxent in Maryland. Patuxent subsequently, and most effectively, applied captive propagation to the conservation of the endangered Mississippi Sandhill Crane. Following the example of Patuxent, a private organization, the International Crane Foundation, was established in Baraboo, Wisconsin in 1973 with the intention of helping all 15 species of cranes. In 1979, the Soviets established a breeding center for Siberian Cranes near Moscow at the Oka State Nature Reserve, and in 1984, the Royal Forest Department of Thailand set up a center near Bangphra for the captive management of Eastern

Sarus Cranes. Other centers, notably the Baltimore Zoo, Beijing Zoo, Kushiro Crane Park in Japan, the London Zoological Society, the National Zoo in Washington, D.C., the Bronx Zoo in New York City, Tama Zoo in Japan, and Vogelpark Walsrode in Germany, have all made significant contributions to the captive management of cranes. The addresses of many other institutions with crane colonies can be obtained through ISIS (International Species Information System; see Chapter 10).

Some **longevity** records of captive cranes are remarkable. A male Siberian Crane (Fig. 1.19) that died from an injury in 1988 was captured, presumably as an adult, early in the 20th century. He had survived the two World Wars by residing at a zoo in Switzerland, and finally, in his late 70's, he fathered chicks at ICF through artificial insemination. In the studbook of the White-naped Crane (Sheppard 1990), reference is made to longevity records of more than 67 years and more than 64 years with breeding of birds over 60. Other remarkable records include a wild trapped female Siberian Crane which survived 61 years and 9 months at the Philadelphia Zoo (Davis 1969), a Wattled Crane at the New York Zoological Society that produced eggs over a 33-year period (Conway and Hamer 1977), and a Eurasian Crane which lived in a zoo for almost 43 years (Mitchell 1911).

Longevity records for wild cranes are unknown because marking individual cranes for identification purposes did not begin until recently. Because life in the wild is more hazardous, it is unlikely that wild cranes survive as long as their captive counterparts.

Status and Conservation

Because most cranes are highly visible at great distances and vulnerable to the loss and degradation of their wetland and grassland habitats, populations of most species have been reduced to a small fraction of their former numbers (Table 1.3) (Archibald and Meine 1995; Meine and Archibald *In prep.*). Seven of the fifteen species are considered threatened at the species level, while several additional subspecies are also at risk of extinction. It is no surprise that the four white species (Siberian, Red-crowned, Black-necked, and Whooping Cranes) are the most endangered. These species are not only the most easily seen, and thus shot, but they are also the most dependent upon aquatic habitats.



FIG. 1.19 Wolf, a 70+ year old Siberian Crane at ICF

PHOTO LYNN M. STONE

The Whooping Crane has staged a remarkable (although incomplete) recovery. Birds in the migratory population have come back from a low point of about 15 or 16 birds in 1941 to 133 cranes during the winter of 1992–93. These cranes breed in the vicinity of Great Slave Lake in northwestern Canada, and winter 2,500 miles away on the coast of Texas. There are also a few wild Whooping Cranes in an experimental flock (Fig. 1.20) in the western United States. These are all that remain from 289 eggs cross-fostered to Sandhill Cranes beginning in 1975. High chick mortality, disease, collisions with powerlines, and sexual imprinting on Sandhill Cranes have led to the discontinuation of the effort. Eggs for this flock, which peaked at about 35 birds in 1985, were produced in captivity at Patuxent (73 eggs) and collected from the wild cranes in Canada (216 eggs from 1975–1983; Ellis et al. 1992). Since 1985, one viable fertilized egg has been moved from nests where two viable eggs were present. These “second eggs” were placed in nests where all eggs failed to show signs of life (Lewis 1986). Eggs removed from the latter category were then collected. Some of these, however, proved to be fertile and were hatched at the captive breeding centers. In addition to the wild birds, there are now over 120 Whooping Cranes in captivity. Nearly all of these birds are at Patuxent or ICF, with a third captive breeding center recently established at the Calgary Zoo in Canada. There are also about 50 wild birds in a second experimental population in the Kissimmee Prairie in Florida where since 1993 captive-reared cranes have been released into a non-migratory setting.

There are two geographically isolated populations of Red-crowned Cranes: a group of 600–650 cranes in southeastern Hokkaido, Japan, with several more on

TABLE 1.3

Approximate size of crane populations.¹

SPECIES OR SUBSPECIES	WILD	CAPTIVITY	STATUS ²
Black Crowned Crane	70,000	450	Threatened
Gray Crowned Crane	90,000	1,200	Non-endangered
Wattled Crane	14,000	172	Threatened
Blue Crane	21,000	1,000	Threatened
Demoiselle Crane	250,000	1,000	Non-endangered
Siberian Crane	3,000	115	Endangered
Sandhill Crane (all races)	700,000	500	Non-endangered
Cuban Sandhill Crane	150	?	Endangered
Mississippi Sandhill Crane	120	40	Endangered
White-naped Crane	5,000	400	Endangered
Sarus Crane (all races)	20,000	350	Non-endangered
Eastern Sarus Crane	1,000	50	Endangered
Brolga	25,000	33	Non-endangered
Eurasian Crane (all races)	225,000	280	Non-endangered
Hooded Crane	10,000	100	Endangered
Black-necked Crane	5,800	90	Endangered
Red-crowned Crane	1,800	750	Endangered
Whooping Crane	170	120	Endangered

¹ Approximate size of world populations, 1995.

² Status: Endangered, likely to become extirpated in the wild during the next century if present population trends continue; Threatened, threatened with eventual extirpation in the wild; Non-endangered, populations generally stable or declining only in a portion of their range.

the neighboring Kurile Islands, now part of Russia, and a population of perhaps 1,000 birds on mainland Asia (Feng and Li 1985; Masatomi et al. 1989; Anonymous 1991). The island population migrates locally from the marshes to several artificial feeding stations near the city of Kushiro. Aided by feeding programs initiated by the local people and now supported by the government, this population has grown to its present size from about 30 birds in 1952. The mainland flock migrates to the Korean peninsula and to coastal wetlands of China just north of the mouth of the Yangtze River. The wetlands where these cranes breed in northern China, southeastern Siberia, and Japan are valuable for agricultural development (Archibald 1987). Wetland loss is the major limiting factor for the species. Japan's first wetland national park, Kushiro Marsh National Park, and one of China's first protected areas, Zhalong Nature Reserve, have been established to protect major nesting areas of



FIG 1.20 Gray's Lake, Idaho, where Whooping Crane eggs were cross-fostered to Sandhill Cranes.

PHOTO SCOTT R. DERRICKSON

these cranes. Red-crowned Cranes are popular exhibit birds in zoos, and they breed readily in captivity.

Siberian Cranes breed in the Arctic of both eastern and western Russia (Fig. 1.21) and winter in Iran (ca 10 birds), India (5-10 birds), and China (ca 3000 birds: K. Ozaki, Yamashina Institute for Ornithology, Abiko City, Japan, personal communication). They are exclusively dependent on wetlands for their breeding and their wintering grounds. Hunting continues to threaten the survival of the remnant flock that migrates through heavily hunted regions of Afghanistan and Pakistan. Loss of wetlands on the wintering grounds and migration staging areas has undoubtedly contributed to the decline of this species. A proposed dam across the Yangtze River poses a threat to the wintering grounds of the majority of Siberian Cranes. With difficulty, Siberian Cranes have been induced to reproduce in captivity at ICF in the United States, at the Oka State Nature Reserve in Russia, at Beijing Zoo in China, and at Vogelpark Walsrode in Germany.

Black-necked Cranes, believed to number about 5,800, breed in freshwater wetlands scattered across the Tibetan Plateau. In winter they migrate to slightly lower elevations in southern Tibet, Yunnan and Guizhou Provinces of China, and several valleys in Bhutan. This species has declined due to hunting on the breeding and wintering areas in China in recent decades and the loss of barley fields and wetlands in which the cranes forage in winter. Several pairs of captive Black-necked Cranes breed at Beijing and Xining zoos in China, and single pairs breed at Vogelpark Walsrode in Germany and at ICF in the United States.

The continuing increase in human numbers, particularly in southern Asia and throughout most of Africa, increasingly threatens the wetlands and grasslands needed by cranes (Archibald and Mirande 1985). But humans can also improve the chances for the survival of cranes through habitat protection, education, and reintroduction. Husbandry will play a central role in this broad conservation agenda. If proper husbandry and genetic management practices are followed, captive breeding can perhaps indefinitely maintain viable populations of each crane species and provide birds for reintroduction efforts. During the past two decades, Patuxent, ICF, Oka State Nature Reserve, Beijing Zoo, Bronx Zoo, and other zoos have developed techniques for the successful management of cranes in captivity. Much of that valuable information is presented in this volume.



FIG 1.21 *Siberian Crane marshes in western Siberia.*

PHOTO DAVID H. ELLIS

Literature Cited

- Allan, D. G. 1995. [Blue Crane biology]. In R. D. Bielfuss, editor. Proceedings of the African Crane and Wetland Training Workshop. International Crane Foundation, Baraboo, Wis. *In press.*
- Allen, R. P. 1952. The Whooping Crane. Research Report No. 3, National Audubon Society, New York. 246 pp.
- Allen, R. P. 1956. A report on the Whooping Crane's northern breeding grounds. National Audubon Society, New York. 60 pp.
- Alonso, J. A., J. P. Veiga, and J. C. Alonso. 1984. Familienaufklärung und Abzug aus dem Winterquartier beim Kranich *Grus grus*. *Journal für Ornithologie* 125:69-74. [In German with English summary. English translation available from ICF.]
- Anonymous. 1991. Winter counts of endangered cranes. *ICF Bugle* 18(4):8.
- Archibald, G. W. 1976a. The unison call of cranes as a useful taxonomic tool. Ph.D. dissertation, Cornell University, Ithaca, New York. 167 pp.
- Archibald, G. W. 1976b. Crane taxonomy as revealed by the unison call. Pages 225-251 in J. C. Lewis, editor. Proceedings International Crane Workshop. International Crane Foundation, Baraboo, Wis.
- Archibald, G. W., and C. Meine. 1995. Family Gruidae. In J. del Hoyo and A. Elliot, editors. Handbook of the birds of the world. Vol. 2. Lynx Edicions, Barcelona.
- Archibald, G. W., and C. M. Mirande. 1985. Population status and management efforts for endangered cranes. Pages 586-602 in Proceedings 50th North American Wildlife Natural Resources Conference.
- Archibald, G. W., and S. R. Swengel. 1987. Comparative ecology and behavior of Eastern Sarus Cranes and Brolgas in Australia. Pages 107-116 in J. C. Lewis, editor. Proceedings 1985 Crane Workshop. Platte River Whooping Crane

- Habitat Maintenance Trust and U.S. Fish and Wildlife Service, Grand Island, Nebr.
- Archibald, K. 1987. The conservation status of the breeding ground of the Red-crowned Crane in Hokkaido, Japan. Pages 63-86 in G. W. Archibald and R. R. Pasquier, editors. Proceedings 1983 International Crane Workshop. International Crane Foundation, Baraboo, Wis.
- Bennett, A. J. 1978. Ecology and status of Greater Sandhill Cranes in southeastern Wisconsin. M.S. thesis, University of Wisconsin, Stevens Point. 110 pp.
- Bishop, M. A. 1984. The dynamics of subadult flocks of Whooping Cranes wintering in Texas, 1978-79 through 1982-83. M.S. thesis, Texas A&M University, College Station. 127 pp.
- Bishop, M. A. 1994. [Black-necked Crane biology]. Unpublished reports at International Crane Foundation, Baraboo, Wis.
- Blaauw, F. E. 1897. A monograph of the cranes. E. J. Brill, London, England and Leiden, Netherlands. 69 pp.
- Brodkorb, P. 1967. Catalogue of fossil birds. Bulletin of the Florida State Museum 11:145-153.
- Brown, L. H., and P. L. Britton. 1980. The breeding seasons of East African birds. East Africa Natural History Society, Nairobi, Kenya.
- Cheng, Tso-hsin. 1981. Cranes of China. Pages 47-48 in J. C. Lewis and H. Masatomi, editors. Crane research around the world. International Crane Foundation, Baraboo, Wis.
- Conway, W., and A. Hamer. 1977. A 36-year laying record of a Wattled Crane at New York Zoological Park. Auk 94:786-787.
- Cyrus, D., and N. Robson. 1980. Bird atlas of Natal. Natal University Press, Pietermaritzburg, South Africa. 320 pp.
- Davis, M. 1969. Siberian Crane longevity. Auk 86:347.
- Derrickson, S. R., and J. W. Carpenter. 1987. Behavioral management of captive cranes—factors influencing propagation and reintroduction. Pages 493-511 in G. W. Archibald and R. F. Pasquier, editors. Proceedings of the 1983 International Crane Workshop. International Crane Foundation, Baraboo, Wis.
- Doughty, R. W. 1989. The return of the Whooping Crane. University of Texas Press, Austin. 182 pp.
- Drewien, R. C. 1973. Ecology of Rocky Mountain Greater Sandhill Cranes. Ph.D. dissertation, University of Idaho, Moscow. 82 pp.
- Ellis, D. H., J. C. Lewis, G. F. Gee, and D. G. Smith. 1992. Population recovery of the Whooping Crane with emphasis on reintroduction efforts: past and future. Proceedings North American Crane Workshop 6:142-150.
- Ellis, D. H., S. R. Swengel, G. W. Archibald, and C. B. Kepler. *In prep.* A sociogram for the cranes of the world.
- Feng Ke-min and Li Jin-lu. 1985. Aerial surveys on the Red-crowned Cranes (*Grus japonensis*) and other rare water birds. Pages 17-34 in H. Masatomi, editor. International spring censuses on *Grus japonensis* (Red-crowned Crane) in 1984. Wild Bird Society of Japan, Tokyo.
- Gichuki, N. 1995. [Grey Crowned Crane biology]. In R. D. Biefuss, editor. Proceedings of the African Crane and Wetland Training Workshop. International Crane Foundation, Baraboo, Wis. *In press.*
- Herter, D. R. 1982. Staging of Sandhill Cranes on the eastern Copper River Delta, Alaska. Pages 273-280 in J. C. Lewis, editor. Proceedings 1981 International Crane Workshop. National Audubon Society, Tavernier, Florida.
- Hunt, H., and R. Slack. 1987. Winter foods of the Whooping Crane based on stomach content analyses. Pages 217-218 in J. C. Lewis, editor. Proceedings 1985 Crane Workshop. Platte River Whooping Crane Habitat Maintenance Trust, Grand Island, Nebr.
- Hyde, D. O. 1957. Crane notes. Blue Jay 15:19-21.
- Ingold, J. L. 1984. Systematics and evolution of the cranes (Aves: Gruidae). Ph.D. dissertation, Miami University, Oxford, Ohio. 62 pp.
- Iverson, G. C., T. C. Tacha, and P. A. Vohs. 1982. Food contents of Sandhill Cranes during winter and spring. Pages 95-98 in J. C. Lewis, editor. Proceedings 1981 International Crane Workshop. National Audubon Society, Tavernier, Fla.
- Johnsgard, P. A. 1983. Cranes of the world. Indiana University Press, Bloomington. 257 pp.
- Johnson, D. N., and P. R. Barnes. 1991. The breeding biology of Wattled Cranes in Natal. Pages 377-386 in J. T. Harris, editor. Proceedings 1987 International Crane Workshop. International Crane Foundation, Baraboo, Wis.
- Koga, T. 1961. Studies on the reproduction of cranes, especially on their artificial incubation and breeding. Journal of the Japanese Association of Zoological Gardens and Aquariums 3(3):51-58. [In Japanese with English summary.]
- Koga, T. 1976. Increasing captive production of Japanese and White-naped Cranes. Pages 351-355 in J. C. Lewis, editor. Proceedings International Crane Workshop. Oklahoma State University Printing, Stillwater.
- Konrad, P. M. 1981. Status and ecology of Wattled Crane in Africa. Pages 220-237 in J. C. Lewis and H. Masatomi, editors. Crane research around the world. International Crane Foundation, Baraboo, Wis.
- Konrad, P. M. 1987. Rainy season ecology of South African Grey Crowned Cranes in the Luangwa Valley, Zambia. Pages 337-344 in G. W. Archibald and R. R. Pasquier, editors. Proceedings 1983 International Crane Workshop. International Crane Foundation, Baraboo, Wis.
- Krajewski, C. 1988. Phylogenetic relationships among cranes (Aves: Gruidae) based on DNA hybridization. Ph.D. dissertation, University of Wisconsin, Madison. 342 pp.
- Kuyt, E. 1979. Banding of juvenile Whooping Cranes and discovery of the summer habitat used by nonbreeders. Pages 109-111 in J. C. Lewis, editor. Proceedings 1978 Crane Workshop. Colorado State University Printing Service, Fort Collins.
- Kuyt, E. 1987. Management and research of Whooping Cranes, 1965-1982. Pages 365-1982 in G. W. Archibald and R. F. Pasquier, editors. Proceedings of the 1983 International Crane Workshop. International Crane Foundation, Baraboo, Wis.
- Kuyt, E., and J. P. Goossen. 1987. Survival, age composition, sex ratio, and age at first breeding of Whooping Cranes in Wood Buffalo National Park, Canada. Pages 230-244 in J. C. Lewis, editor. Proceedings 1985 Crane Workshop. Platte River Whooping Crane Habitat Maintenance Trust and U.S. Fish and Wildlife Service, Grand Island, Nebr.

- Layne, J. N. 1982. Status of sibling aggression in Florida Sandhill Cranes. *Journal of Field Ornithology* 53:272-274.
- Lewis, J. C. 1974. Ecology of the Sandhill Crane in the southeastern Central Flyway. Ph.D. dissertation, Oklahoma State University, Stillwater. 213 pp.
- Lewis, J. C. 1986. The Whooping Crane. Pages 659-676 in R. C. DiSilvestro, editor. Audubon Wildlife Report 1986. National Audubon Society, New York.
- Li Dehao, Zhou Zhijun, We Zhikang, Li Zhumei, and Wang Youhui. 1991. On the structure and behavior of the breeding population of Black-necked Cranes in Songpan Meadow of Sichuan Province. Pages 83-87 in J. Harris, editor. Proceedings 1987 International Crane Workshop. International Crane Foundation, Baraboo, Wis.
- Littlefield, C. D. and R. A. Ryder. 1968. Breeding biology of the Greater Sandhill Crane on Malheur National Wildlife Refuge, Oregon. *Transactions of the North American Wildlife and Natural Resources Conference* 33:444-454.
- Makatsch, W. 1970. Der Kranich. Die Neve Brehn Bucherei 229:28-81. Wittenberg, Germany.
- Masatomi, H. 1970-1974. Ecological studies on the Japanese Crane, *Grus japonensis*. *Journal of Bibai Agricultural Engineering College* Part I (1970) 1:37-45; Part II (1971) 2:93-111; Part III (1972a) 3:153-161; Part IV (1972b) 4:139-152; Part V (1974) 5:1-16.
- Masatomi, H., and T. Kitagawa. 1975. Bionomics and sociology of Tancho or the Japanese Crane, *Grus japonensis*. II Ethogram. *Journal of the Faculty of Science, Hokkaido University, Series VI, Zoology* 19:834-878.
- Masatomi, H., K. Momose, and M. Takeshita. 1989. Wintering population of the tancho *Grus japonensis* in Hokkaido, 1987-'88. *Journal of Environmental Science Laboratory, Senshu University-Hokkaido* 1:73-82.
- McNulty, F. 1966. The Whooping Crane. E. P. Dutton and Co., New York. 190 pp.
- Meine, C., and G. W. Archibald. *In prep.* Action plan for the conservation of cranes. IUCN, Gland, Switzerland.
- Mitchell, P. C. 1911. On longevity and relative viability in mammals and birds, with a note on the theory of longevity. *Proceedings of the Zoological Society of London*, pages 425-548.
- Mullins, W. H., and E. G. Bizeau. 1978. Summer foods of Sandhill Cranes in Idaho. *Auk* 95:175-178.
- Nesbitt, S. A. 1975. Voice maturity in Sandhill Cranes. *Florida Field Naturalist* 3:19.
- Nesbitt, S. A. 1989. The significance of mate loss in Florida Sandhill Cranes. *Wilson Bulletin* 101:648-651.
- Nesbitt, S. A. 1992. First reproductive success and individual productivity in Sandhill Cranes. *Journal of Wildlife Management* 56:573-577.
- Nesbitt, S. A., and G. W. Archibald. 1981. The agonistic repertoire of Sandhill Cranes. *Wilson Bulletin* 93:99-103.
- Nesbitt, S. A., and A. S. Wenner. 1987. Pair formation and mate fidelity in Sandhill Cranes. Pages 117-122 in J. C. Lewis, editor. Proceedings 1985 Crane Workshop. Platte River Whooping Crane Habitat Maintenance Trust and U.S. Fish and Wildlife Service, Grand Island, Nebr.
- Novakowski, N. W. 1966. Whooping Crane population dynamics on the nesting grounds, Wood Buffalo National Park, Northwestern Territories, Canada. Canadian Wildlife Service, Research Report Series 1. 20 pp.
- Peters, J. C. 1934. Check-list of the birds of the world. Vol. II. Harvard University Press, Cambridge, Mass. 401 pp.
- Pomeroy, B. S. 1980. Aspects of the ecology of Crowned Cranes *Balearica regulorum* in Uganda. *Scopus* 4:29-35.
- Prange, H. D., J. S. Wasser, A. S. Gaunt, and S. L. L. Gaunt. 1985. Respiratory responses to acute heat stress in cranes: the effects of tracheal coiling. *Respiratory Physiology* 62:95-103.
- Radke, M. F., and W. R. Radke. 1986. Breeding by a two-year old Sandhill Crane. *Western Birds* 17:192-193.
- Sauey, R. T. 1985. The range, status, and winter ecology of the Siberian Crane *Grus leucogeranus*. Ph.D. dissertation, Cornell University, Ithaca, New York. 428 pp.
- Sheppard, C. 1990. International Studbook of the White-naped Crane, *Grus vipio*, as of December 1989. New York Zoological Society, New York.
- Stephenson, J. D. 1971. Plumage development and growth of young Whooping Cranes. M.S. thesis, Oregon State University, Corvallis. 56 pp.
- Tacha, T. C. 1988. Social organization of Sandhill Cranes from mid-continental North America. *Wildlife Monograph* 99:1-37.
- Tarboton, W. R. 1984. The status and conservation of the Wattled Crane in the Transvaal. Pages 665-679 in J. Ledger, editor. Proceedings of the Fifth Pan African Ornithological Congress. South African Ornithological Society, Johannesburg.
- Taverner, P. A. 1929. The red plumage coloration of the Little Brown and Sand-Hill Cranes, *Grus canadensis* and *mexicanus*. *Auk* 46:228-230.
- Uhler, F. M., and L. N. Locke. 1969. A note on the stomach contents of two Whooping Cranes. *Condor* 52:216.
- Van Ee, C. A. 1966. Notes on the breeding behaviour of the Blue Crane, *Tetrapteryx paradisea*. *Ostrich* 37:23-29.
- Voss, K. 1976. Behavior of the Greater Sandhill Crane. M.S. thesis, University of Wisconsin, Madison. 137 pp.
- Walkinshaw, L. H. 1949. The Sandhill Cranes. *Cranbrook Institute Science Bulletin* 29, Bloomfield Hills, Mich. 202 pp.
- Walkinshaw, L. H. 1964. The African Crowned Cranes. *Wilson Bulletin* 76:355-377.
- Walkinshaw, L. H. 1965. One hundred thirty-three Sandhill Crane nests. *Jack-Pine Warbler* 43:136-143.
- Walkinshaw, L. H. 1973. Cranes of the world. Winchester Press, New York. 370 pp.
- Whymer, C. 1909. Egyptian birds for the most part seen in the Nile Valley. A. and C. Black, London. 221 pp.
- Winter, S. W. 1991. The Demoiselle Crane in the agricultural landscape of the Ukrainian steppe zone. Pages 285-294 in J. Harris, editor. Proceedings 1987 International Crane Workshop. International Crane Foundation, Baraboo, Wis.
- Wood, D. S. 1979. Phenetic relationships within the family Gruidae. *Wilson Bulletin* 91:384-399.

